ORIGINAL ARTICLE

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Innate versus learned recognition of conspecifics in great spotted cuckoos *Clamator glandarius*

Abstract When birds raised by another species become adults, they (if they are non-brood-parasitic species) usually attempt to mate with birds of their foster species rather than with birds of their own species, a phenomenon called sexual imprinting. Avian brood parasites lay their eggs in nests of other species (the hosts) that rear the young, but the problem of sexual imprinting among brood parasites has generally been neglected, and brood parasites have been considered as an exception among birds. Here, we show, with data from field observations and field experiments, firstly, that adult great spotted cuckoos *Clamator glandarius* sometimes maintain contact with both older nestling and fledgling cuckoos. Adult cuckoos visited parasitized nests during the last days of the nestling period (5 observations) and, when parasitic chicks left the nest, adult cuckoos maintained contact with the young (14 observations). Adults and fledgling cuckoos communicated vocally (5 observations), and an adult great spotted cuckoo even fed a parasite fledgling in two cases. Secondly, when experimentally cross-fostered in nests of magpie *Pica pica* hosts outside the parasite breeding range (thus avoiding visual and acoustic communication with adult cuckoos), young cuckoos did not learn to recognize their own species when only one cuckoo chick was introduced per nest, but they learnt to recognize conspecifics when two cuckoos were reared together. This means that young great spotted cuckoos apparently must learn to recognize conspecifics, that is, recognition is not innate. Social interactions between adult brood parasites and young have also been reported in other brood parasites; thus, brood parasites are probably not an exception to the general phenomenon of imprinting, and young brood parasites may need to be imprinted on conspecifics, although more studies on other brood parasite species are needed to confirm this.

Introduction

Early learning of parental plumage characteristics enables young birds subsequently to recognize members of their own species (Spalding 1873; Lorenz 1935; Bateson 1966; Salzen 1998). When birds are raised by another species, this imprinting has immediate consequences for filial and social behaviour (so-called filial imprinting), and when they become adults, they attempt to mate with birds of their foster species rather than with birds of their own species, a phenomenon called sexual imprinting (Spalding 1873; Lorenz 1935; Sluckin 1965; Bateson 1966; Salzen 1998). This type of imprinting has proved to be more widespread than previously assumed, being found virtually whenever investigated, and should thus be considered the rule among birds (ten Cate et al. 1993).

Lorenz (1935) claimed that imprinting occurs during a brief critical period in development. This sensitive period ends before the chick is likely to mix with birds other than its parents or siblings; that is, the sensitive period covers the most suitable time to receive the right information (Bateson 1979). Another relevant point is that the presence of siblings is very important to a bird in establishing a social preference for its own species (Lorenz 1935; Kruijt et al. 1983). In fact, Bateson (1979) suggested that chicks delay learning about their siblings until they are old enough for their juvenile characteristics to provide a reliable indication of their adult appearance.

Brood parasitism is rare among birds, only 1% of species being brood parasites (Payne 1977; Rothstein 1990). Avian brood parasites lay their eggs in the nests of other bird species that incubate the parasitic eggs and rear the young (Payne 1977; Rothstein 1990). Hence, obligate brood parasites rely entirely on the exploitation of parental care provided by their host, and adult parasites are assumed not to provide any parental care for their offspring (Payne 1977; Rothstein 1990).

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Young brood parasites are assumed never to encounter adult conspecifics but nevertheless to become sexually imprinted on conspecifics (Payne 1977; Rothstein 1990). Brood parasites have therefore been considered as an exception among birds: thus, in brood parasite species, conspecific recognition has been assumed to be innate (Tinbergen 1951; Hamilton and Orians 1965). Tinbergen (1951) concluded for the European cuckoo (*Cuculus canorus*), that recognition and selection of a conspecific mate was innate because young cuckoos never encountered an adult cuckoo. This problem of whether sexual imprinting among brood parasites is learned or innate has generally been neglected both in the literature on brood parasites (Payne 1977; Rothstein 1990), and in the literature on imprinting (Sluckin 1965; Salzen 1998).

There have been some studies of conspecific recognition in brown-headed cowbirds (*Molothrus ater*). Graham and Middleton (1989) discovered that hand-reared cowbird fledglings began to be able to discriminate conspecifics soon after fledging. King and West (1977) discovered that captive female cowbirds, reared in the laboratory in complete auditory and visual isolation from other cowbirds, adopted copulatory postures when they were exposed to a recording of a male cowbird courtship song. Later, they (West and King 1988) suggested that female cowbirds can impart relevant vocal skills to males – that is, females can shape the content of the males' vocal repertoires through visible responses. However, recently, new data on cowbirds have suggested an important role for social transmission from older to younger males (Freeberg et al. 1995).

The great spotted cuckoo *Clamator glandarius* is an obligate avian brood parasite (a species which is not able to build its own nests and rear its own offspring) which in Europe mainly parasitizes the magpie *Pica pica*. In Hoya de Guadix, Spain, for example, 37% of the parasitized nests received only one cuckoo egg, but 63% received two or more (mean = 2.4 great spotted cuckoo eggs per host nest; Soler et al. 1998). Parasitic eggs hatch before those of the host, but unlike other cuckoos, the *C. glandarius* chick (or chicks) does not eject host eggs or nestlings (Soler 1990). Great spotted cuckoos breeding in Europe overwinter in Africa south of the Sahara Desert (Cramp 1985). Individuals usually return to southern Spain in late February or early March (Soler 1990). Adults leave the breeding areas at the beginning of July, while juveniles usually leave 2 months later, though juveniles that leave the nest earlier sometimes leave at the same time as adults (Soler et al. 1994). Fledgling great spotted cuckoos are very sedentary, each group usually occupying the same small area (of only 0.68 ha; Soler et al. 1995) where they wait for the magpies to feed them throughout the season (Soler et al. 1994). Juveniles of nidicolous bird species usually start to feed themselves soon after leaving the nest. However, unexpectedly, we never saw *C. glandarius* juveniles feeding themselves; rather, cuckoo fledglings were fed by the magpies until the fledglings left the area (on average 33 days; Soler et al. 1994).

In a previous study (Soler et al. 1995), we found that fledgling cuckoos characteristically aggregated with other fledgling cuckoos reared in other magpie nests, whereas magpie fledglings never joined these groups. Group size ranged from two to five fledgling cuckoos (only 2 out of 62 cuckoo fledglings remained alone). Cuckoo fledglings aggregated between 2 and 9 days after leaving the nest, and the average distance between the nest in which they were reared and the centre of the group area was 205 m (range 4–1032 m) (Soler et al. 1995). For these reasons, in our experiments, this aggregation is considered normal cuckoo fledgling behaviour. Cuckoo fledglings that do not join other cuckoo fledglings but remain with their foster siblings in the territory of their foster parents will be considered not to be behaving like normal fledgling cuckoos (the two cuckoo fledglings which remained alone in our study in the Hoya de Guadix did not join any magpie fledglings; Soler et al. 1995).

The aims of this paper are, first, to show that adult great spotted cuckoos sometimes visit both older nestling (more than 14 days old) and fledgling cuckoos. Second, because apparent "parental behaviour" by great spotted cuckoos is only sporadically observed (this study), andis not sufficiently frequent to increase the survival probabilities of an offspring, we hypothesized that this contact between the adult cuckoo and nestling or fledgling might be a carryover from ancestral brood care to counteract sexual imprinting by parasite chicks on their foster parents. Two predictions from this hypothesis are experimentally tested:

1. If young great spotted cuckoos need to be imprinted on their own species (i.e. recognition is not innate), cuckoo chicks cross-fostered in magpie nests located in an area of allopatry with cuckoos should not behave like fledgling cuckoos from naturally parasitized nests (after conspecific imprinting).
2. If the presence of siblings is also important to birds in establishing social preference for their own species (Lorenz 1935; Kruijt et al. 1983), then two nestling cuckoos introduced into the same host nest in an area of allopatry should later behave like fledgling cuckoos after conspecific imprinting.

Materials and methods

Observations

Relationships between adult and fledgling cuckoos were observed mainly during 1991 and 1992, when 19 and 21 great spotted cuckoo fledglings, respectively, were fitted with radiotransmitters and observed systematically while adult cuckoos were present in the Hoya de Guadix study area (between 25 May and 8 August in both years) (see Soler et al. 1994, 1995, for further details).

The Hoya de Guadix (southern Spain, 38°18′N, 3°11′W) is a high-altitude plateau at about 1000 m above sea level (a.s.l.). The vegetation is sparse, but there are many groves of almond trees (*Prunus dulcis*) in which

magpies nest at high density, and this magpie population is heavily parasitized by the great spotted cuckoo (parasitism rate = 54.8%, $n = 766$; Soler et al. 1998).

Experiments

The experiments were conducted in (1) Torres del Segre (Lleida, Spain, 41°32′N, 0°31′E) within the breeding range of the great spotted cuckoo, but free of parasitism (parasitism rate = 0%), during 1994 and 1995; and (2) Freneusse (France, 49°00′N, 2°30′E) outside the breeding range of the great spotted cuckoo, during 1996 and 1997.

Two different experiments were performed, in both of which cuckoo nestlings were introduced into magpie nests in areas of allopatry with cuckoos, and the behaviour of the cuckoo fledglings later recorded. In experiment 1, one cuckoo nestling was introduced per magpie nest, and this was conducted four times: in Torres del Segre during 1994 and 1995, and in Freneusse during 1996 and 1997. Experiment 2, in which two cuckoo nestlings were introduced per magpie nest, was performed in Torres del Segre during 1994.

Only cuckoo chicks reared with no experience of other cuckoo nestlings, i.e. reared alone or together with magpie chicks, were used. They were collected from the Hoya de Guadix study area when they were 7–10 days old, without previous contact with adult cuckoos. The experimental schedule involved transporting each chick inside a box from Guadix to Torres del Segre ($n = 36$) or to Freneusse ($n = 24$). During each trip, no more than four chicks were transported. To prevent vocal contact, each box was placed as far as possible from the others (each in one corner of the car) and the radio was put on with the volume at a high level. Most of the distance in each case was covered during the night, but during the daytime, each chick was fed with minced cow heart outside the car, so that other chicks could not hear the begging calls of the chick that was being fed. The cuckoo nestlings were placed in previously identified nests with magpie chicks of a size similar to or smaller than the cuckoo chick, to increase the probability of the cuckoo chick being reared successfully. Experimental nests were chosen in areas with a high density of magpie nests to ensure that cuckoo chicks would have the opportunity of meeting other cuckoo chicks reared in neighbouring nests. Later, when they were 14 or 15 days old, in nests which had not been predated, young cuckoos were provided with radio-transmitters and systematic observations were made (once per week during experiments in 1994–1996 and daily during experiments in 1997) of each fledgling for 1–2 h. A total of 38 cuckoo fledglings (13 in 1994, 10 in 1995, 5 in 1996, 10 in 1997) were fitted with radio-transmitters 1 or 2 days before fledging. Each radio-transmitter weighed 4 g (including back-pack harness) with a trailing 20 cm wire antenna (Biotrack, Dorset, UK). Transmitters had a range up to 1000 m and a life-span of 10–12 weeks.

We did not use a control for the experimental manipulation, because we believe it was unnecessary for two reasons: firstly, cross-fostered cuckoo chicks in other experimental studies in our study area also joined groups at the fledgling stage (M. Soler, J.J. Soler and J.G. Martinez, unpublished work); and, secondly, the experiment in 1995 showed that, after an adult great spotted cuckoo contacted fledglings, these formed a group (this study).

Results

Observational evidence

Intensive field work in the Hoya de Guadix study area showed that the great spotted cuckoo exhibited behaviour which could be categorized in the following way. (In all the observations described here, different nests, adults and/or fledglings were involved.)

1. Adult cuckoos visited parasitized nests during the last days of the nestling period, when parasitic chicks were 14 or more days old (5 observations).
2. When parasite chicks left the nest, adult cuckoos maintained contact with the young by perching in the same tree or nearby and sometimes approaching the young cuckoos and vocalizing (14 observations); sometimes the adult cuckoo, carrying a leaf or a small stick in its beak, was observed following the cuckoo fledgling into the tree canopy (4 observations, 28.6%). We do not know the reason for this behaviour, but offering of vegetable matter has also been recorded in cuckoo males while they were courting females (Soler 1990).
3. Before perching together, adult and fledgling cuckoos communicated vocally (5 observations); in all cases both members vocalized – the adult first, while approaching the area, and immediately afterwards the fledgling, whose call induced the adult to remain nearby (this vocal interaction might be repeated twice or more). Adult cuckoos also gave alarm calls that silenced the fledgling (2 observations).
4. An adult great spotted cuckoo even fed a parasite fledgling (2 observations).

These observations show that the associations were initiated by the adult, but young cuckoos may have biases to respond to species-specific cues.

In one of the cases where one adult and one fledgling cuckoo communicated vocally (see point 3 above), it was known that the adult was the mother of the chick (she had been provided with a radiotransmitter and she was recorded laying that egg), and thus, it is not unreasonable to suppose that these contacts observed in the Hoya de Guadix between adult and fledgling cuckoos were between parents and their offspring (but see below, experiment in Torres del Segre).

Experimental evidence

The two predictions in the Introduction, derived from the hypothesis that social interactions between adults and

young cuckoos occur because young great spotted cuckoos may need to be imprinted on conspecifics, were tested in a series of experiments where one or two cuckoo chicks were introduced into magpie nests in areas of allopatry with the cuckoo. Before we present the results, two relevant observations need to be summarized:

First, in the 1995 experiment in Torres del Segre, during the first 2 weeks of the experiment, each fledgling cuckoo ($n = 7$) remained in the territory of its magpie foster parents; however, in the 3rd week, these fledglings aggregated to form two different groups. When we located the first group, of four fledglings, there was one adult great spotted cuckoo nearby, perching in the same tree as two of the fledglings. In the afternoon, we located a second group, of three fledglings, and there was another adult cuckoo nearby (possibly the same, although this is not certain – in any case the adults could not have been related genetically to the fledglings, which came from Hoya de Guadix). That is, we found that a completely unrelated adult great spotted cuckoo made contact with the fledgling cuckoos transported by us to Torres del Segre. (None out of 37 magpie nests found in this area during 1995 was parasitized and no adult great spotted cuckoos had been seen there before). In an area with great spotted cuckoos, cuckoo fledglings aggregate after 2–9 days (Soler et al. 1995), thus the fact that these seven cuckoos did not aggregate for more than 2 weeks indicates that without the presence of adult cuckoos, fledglings do not aggregate.

Second, during the 1997 experiment in Freneusse, each of the three magpie nests from which cuckoo chicks fledged was located in a group of trees. The distance between these groups of trees was consistently less than 120 m. When it was 17 days old, the oldest cuckoo (A) visited the group of trees of another cuckoo fledgling (B) and obtained food from B's magpie foster parents. Its visits were repeated on 4 consecutive days, and one night cuckoo A even roosted in the territory of cuckoo B. However, cuckoo A invariably alternated these visits to the territory of cuckoo B with stays in its own territory. During the 3 days following the visits to B, cuckoo A remained in its territory, and on the 4th day, after a storm, it was found dead (24 days old). When it was 14 days old (the day after cuckoo A died), cuckoo B visited the territory of cuckoo A and received food from the magpies. These observations indicate that these two cuckoo fledglings did not show the characteristic aggregation behaviour, because once a group is formed the members are extremely cohesive and they roost together every night (Soler et al. 1995).

Systematic observations of the fledglings gave the following results (Table 1):

1. When two cuckoos were introduced into the same nest, they behaved like cuckoos on leaving the nest (Table 1, experiment in Torres del Segre, 1994). That is, they learnt to recognize their own species.
2. When only one cuckoo was introduced per nest, at fledging they did not join a group (Table 1), even when they met other cuckoo fledglings (see above, com-

Table 1 The four experiments carried out in Torres del Segre (1994 and 1995) within the breeding range of the great spotted cuckoo, and Freneusse (1996, 1997) outside the breeding range of the great spotted cuckoo

	Experiments				
	Torres del Segre (Spain)			Freneusse (France)	
	1994	1994	1995	1996	1997
Experimental treatment (one or two chicks)	Two	One	One	One	One
Transmitters	8	5	10	5	10
Number of cuckoo fledglings that survived at least 2 weeks	4	3	7	3	3
Distance between the two closest fledgling territories (m)	200	600	130	2500	70
Cuckoo fledglings formed groups	Yes	No	No	No	No

ments on the 1997 experiment in Freneusse). Thus, these fledgling cuckoos did not recognize conspecifics when they were reared without any other cuckoo nestling in a nest where we experimentally prevented contact with adult cuckoos.
3. After an adult cuckoo had made contact with cuckoo fledglings reared alone, the fledglings recognized conspecifics even 2 weeks after they had fledged (see above, description of the 1995 experiment in Torres del Segre).
4. Adult cuckoos contacted fledglings even when these fledglings were not the adult's own offspring (see above, description of the 1995 experiment in Torres del Segre).
5. Visiting other magpie territories begging for food may be an innate behavioural pattern of hungry great spotted cuckoo fledglings (see above, description of the 1997 experiment in Freneusse), which has also been suggested for the pallid cuckoo *Cuculus pallidus* (Sealy and Lorenzana 1997). Perhaps obtaining supplementary feeding is a strategy used by some brood parasitic species.

Discussion

The observation that an unrelated adult cuckoo made contact with the fledglings 2 weeks after they left the nest, promoting their aggregation behaviour, suggests that, firstly, the timing of the sensitive phase for sexual imprinting in young cuckoos might be delayed until the reception of the appropriate stimulus, which would represent an adaptation to their brood parasitic way of life. A delay in the timing of the sensitive phase for sexual imprinting has been shown for the brown-headed cowbird (O'Loghlen and Rothstein 1993). Secondly, it means that adults making contact with fledgling cuckoos do not need to be the real parents – that is, adult cuckoos do not restrict contact to their own fledglings. Similarly, Hahn and

Fleischer (1995) reported that 61% of the female-juvenile pairs of brown-headed cowbirds caught in the same trap were unrelated, and thus apparently adult cowbirds also contact fledglings that are not their own. Perhaps adult cuckoos gain advantages even from making contact with unrelated fledglings, because if the adults and juveniles migrate together (as they sometomes do: Soler et al. 1994), the risk of predation for the more experienced adult cuckoo may be lower within such a group (see Kenward 1978).

The fact that fledgling cuckoos did not aggregate when only one was introduced per nest indicates that without the presence of adult cuckoos, fledglings do not aggregate, suggesting that species recognition is not innate. If sexual imprinting were an instantaneous and irreversible process, as proposed by Lorenz (1935), it would be very difficult to understand how a nestling cuckoo could be imprinted on its own species after continuous contact with its foster parents. However, there is empirical evidence showing that imprinting is less rigid than previously believed (Immelmann et al. 1991; Kruijt and Meeuwissen 1991). At present we know that (1) conspecific parents provide more effective imprinting stimuli than do foster parents, by having better-quality interactions with the offspring (ten Cate 1982, 1984; ten Cate et al. 1984; Junco 1993); (2) the optimum period for sensitivity to environmental stimulation may be delayed (O'Loghlen and Rothstein 1993), and is linked to what might functionally be the most suitable period to receive the right information (Bateson 1979); and (3), cross-fostered individuals can be re-imprinted on their own species even in adulthood (Immelmann et al. 1991; Bischoff and Clayton 1991; Kruijt and Meeuwissen 1991). These three points support the idea that adult great spotted cuckoos may, by visiting parasitized nests in the late phase of the nestling period and making contact with fledgling cuckoos, imprint young cuckoos (or re-imprint if the chicks had already been imprinted on the foster parents), if the onset of the sensitive phase is delayed in this species, even when contact is made as late as 2 weeks after fledglings leave the nest. Though mate-choice tests would be the best experimental approach to determine how these associations of fledgling cuckoos with other fledgling cuckoos or magpies actually affect sexual preferences and partner choice, we have shown that young great spotted cuckoos apparently must learn to recognize conspecifics, and this recognition learning is probably related to sexual imprinting.

Visits by adult brood parasites to parasitized nests during the nestling period are relatively frequent in some species, such as the screaming cowbird *Molothrus rufoaxillaris* (Fraga 1992). The feeding of juveniles by adult parasites has been sporadically recorded not only in the great spotted cuckoo (Mundy and Cook 1977; this study), but also in other cuckoo species such as *Cuculus canorus* (Cramp 1985) and *C. pallidus* (Friedmann 1968), in at least four species of the genus *Chrysococcyx: C. lucidus* (Friedmann 1968; Brooker and Brooker 1989), *C. caprius, C. klaas* and *C. cupreus* (Friedmann 1968) and in other genera of parasitic Cuculidae, namely*, Eudynamis, Cacomantis* and *Scythops* (Friedmann 1968). In the genus *Molothrus*, feeding behaviour of parasitic adults has also been recorded (Friedmann 1963), and mixed flocks of adults and recently fledged cowbirds are not uncommon (Hahn and Fleischer 1995). Hahn and Fleischer (1995) found that juvenile and female cowbirds trapped together were probably related in 36% of the cases (although the authors did not discuss the problem of imprinting). This frequently recorded behaviour among adult brood parasites, of maintaining contact with their young, could be interpreted as an effort to promote filial and subsequently sexual imprinting. Though in the brown-headed cowbird there is evidence for one mechanism of innate species identification (King and West 1977), no details were given about three relevant methodological points: (1) how and when the chicks were collected, (2) whether the chicks were collected from nests containing two or more parasitic chicks, and (3) whether they were collected early or late in the nestling period. According to our results, these three possibilities would considerably affect their experimental results.

The information provided in the present study supports the idea that the process of imprinting (or re-imprinting, see above) may be widespread among avian brood parasites. However, this idea has been tested in only one species, the great spotted cuckoo, and additional studies on other brood parasitic species are needed.

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